

39. The Comparative Anatomy of the Tongues of the Mammalia.—VI. Summary and Classification of the Tongues of the Primates. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society.

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INTRODUCTION.

In the five preceding papers of this series I described the structure of the tongues of the Primates and gave a short account of the physiology of the lingual glands. I also drew attention to a number of points bearing on the phylogeny of the tongue. In the present paper I have summarised these observations and pointed out how the lingual characters support systems of classification which have been based on external and skeletal characters.

SUMMARY.

Pigmentation.—Most of the pigmented forms are included in the Cebidæ. The colour, which is yellow, green, brown or bluish-black, especially the latter, is uniformly distributed all over the dorsum, or the pigmented and colourless parts may form definite patterns; in *Ateles grisescens*, for example, there is a white cross on a brown background. The vallate and fungiform papillæ may be pigmented (e. g. in *Hylobates lar*) or colourless, but the lateral organs and central parts of the inferior surface of the tongue are always white. If several examples of each pigmented species are examined it will be seen that the colour varies considerably, so is of no value for purposes of classification. Most specimens of *Cercopithecus patas*, for example, have reddish-yellow tongues, but some tongues are colourless, and the fungiform papillæ of *Cercopithecus tantalus* are yellow or colourless.

The bluish-black colour persists longest in preserving fluids.

Form and Proportions.—Most tongues are conical, but a few are oval, spatulate or rectangular; and shape is of no value for comparative purposes.

In most of the Primates the tongue is long and comparatively narrow, but in *Anthropopithecus troglodytes* and *Gorilla gorilla* the tongue of the young animal is relatively wider than that of the adult. I did not, however, see such variations in *Cercopithecus patas* or *Macacus sinicus*, of which I examined very young and adult examples.

Cunningham showed that the tongue of *Simia satyrus* resembles that of *Homo* most closely in the relative proportions of length and width.

The Apex is round, truncate or pointed, and may or may not have a notch, but the latter is usually absent from the fresh tongue. It is comparatively smooth, or roughened and tubercu-

lated by small conical and fungiform papillæ. The relative quantities of fungiform papillæ on and immediately behind the apex vary; in the Simiidae and Cercopithecidæ they are numerous and thickly clustered, but in the other families they are few and discrete.

In some species of *Lemur* the apex exhibits a number of sharp-pointed processes prolonged forwards from ridges on the inferior surface of the tongue, but these vary even in different examples of each species.

Sulci and Ridges.—Few fresh tongues have median dorsal sulci on the oral part of the dorsum, but many preserved specimens do; and I observed a well-marked median sulcus on the pharyngeal part in *Anthropopithecus troglodytes* alone. The most pronounced mesial dorsal sulcus which I observed occurred in *Mystax ursulus*. Median dorsal ridges are present in some Lemuroidea and Hapalidæ.

Wide, shallow transverse sulci separating low wide transverse ridges are present on the fresh tongues of *Lemur catta* and *Hapale jacchus*; and fine narrow sulci are seen in *Gorilla gorilla* and *Perodicticus potto*. Some of the fine sulci and ridges remind one of the patterns of fissures and ridges on the finger-tips.

The median ventral sulcus is present in most tongues, and is never an artefact induced by preserving fluids as is the dorsal one in bottled specimens. It is narrow and deep, or wide and shallow, and it frequently opens posteriorly into a triangular fossa which receives the upper end of the frenum. In some of the Lemuroidea it receives the median dorsal crest of the sublingua, and it recesses the crest on the dorsal surface of the frenal lamella of *Cebus fatuellus*.

In *Gorilla gorilla*, some species of *Hyllobates* and some of the Lemuroidea it contains a fixed crest; and it has been stated that the crest is a remnant of the sublingua, but the presence of both these structures in some Lemurs would seem to disprove that theory.

Lateral Borders.—The edges of the tongue are sharp, or full and rounded, and increase in thickness from before backwards in most species. Those of *Chiromys madagascariensis* are more massive in proportion to the size of the tongue than those of any other species of the Primates. Of the Pithecooids *Simia satyrus* and *Anthropopithecus* have the most massive lateral borders.

In *Tarsius spectrum*, *Microcebus*, *Chiromys*, and all Lorisidæ and Galagidæ the lateral borders are devoid of lateral organs and, as I hope to show in a future paper, this has an important bearing on phylogeny. In *Gorilla gorilla* and *Simia satyrus* only small parts of the lateral organs are found on the lateral borders, but in all other Primates the greater part is found there.

The conical and fungiform papillæ on the lateral borders are arranged in vertical rows and the points of the former are directed backwards.

Distribution of the Papillæ.—In all Primates except some specimens of *Simia satyrus* and *Symphatanus syndactylus*, some Lemuroidea and *Homo*, papillæ cover the entire dorsum, apex, lateral borders, and a bounding zone of the inferior surface. In all these species there are smooth non-papillary areas on the base of the tongue, and in the Lemurs the area is bisected by the median glosso-epiglottic fold.

The *ventral papillary zone* varies greatly in width, and its characters are of limited value for purposes of classification. It is wide in the Simiidae, Cercopithecidae, and in *Cebus*, *Ateles*, and *Lagothrix*, but is narrow or absent in all other Primates. In species with a wide zone the conical and fungiform papillæ are numerous, but in those with a narrow zone there are few or no fungiforms. In *Gorilla gorilla* many of the fine transverse sulci on the dorsum cut the lateral borders and run inwards on the ventral papillary zone.

The *Circumvallate Papillæ.*—In my paper on the tongues of the Cercopithecidae I showed that all the papillary patterns present in the family will be seen in most species if sufficient examples of each are examined. The whole series may quickly appear or it may be necessary to examine many. I am not prepared, however, to apply this rule to any other family except the Hapalidae, as insufficient specimens have come to hand.

In the following list of papillary patterns, P means two papillæ forming a pair, and D.P. indicates four papillæ arranged in a double pair. The Y type means that there are several papillæ present and does not include forms in which the four papillæ of a double pair are arranged in a Y.

<i>Family.</i>	<i>Patterns of vallate papillæ.</i>				
Simiidae	Y.	T.	V.	Δ.	
Cercopithecidae		T.	V.	Δ.	D.P.
Cebidae			V.	Δ.	P. D.P.
Hapalidae				Δ.	
Lemuridae	Y.			Δ.	D.P.
Lorisidae				Δ.	,
Galagidae				Δ.	P.
Chiromyidae				Δ.	P.
Tarsiidae		Three papillæ arranged in a line.			

One can see, therefore, that the Simiidae and Lemuridae are the only families whose tongues possess more than four papillæ arranged in a Y, and it will be shown later that they differ from all other Primates in other respects.

The papillæ are round or oval on plan and conical on elevation, with the bases of the cones projecting beyond the vallums.

The *Fungiform Papillæ* stretch right across the dorsum, or are absent from the centre thereby forming a dorsal bounding zone. They form a cluster behind the apex, but are arranged in rows

of varying degrees of obliquity behind that. The apical cluster is large in the Simiidae and Cercopithecidae, but in all other families the transverse rows extend far forwards at its expense. In the majority of tongues with large apical clusters there are many fungiform papillae on the ventral papillary zone.

It has been shown by Tuckerman that the fungiform papillae of the apical cluster have many taste-buds.

In some specimens of *Anthropopithecus troglodytes* there is a row of prominent fungiform papillae occupying the mid-dorsal line of the tongue and replacing the median dorsal sulcus.

It is sometimes impossible to tell whether a papilla at the posterior part of the oral division of the dorsum is a large fungiform or small vallate form, for fossa and vallum may be indistinguishable even through a strong lens. Histological examination is the only proof. The fungiform papillae may have no taste-buds or these, if present, lie on the free upper surface of the papilla; in the vallate papillae, on the other hand, the taste-buds never lie on the free upper surface of the papilla, but are deep down on one or both sides of the fossa.

In some tongues there are more fungiform papillae than are visible to the naked eye, for some are entirely concealed by overhanging conical papillae (e. g. *Anthropopithecus troglodytes*).

The fungiform papillae on the ventral zone may be thickly clustered at the apex of the tongue and scanty further back, or *vice versa*, and the examples, and the rows in which they are arranged are close together or discrete.

From the point of view of classification the most important features are the size of the apical dorsal cluster and the presence or absence of the fungiform papillae on the ventral papillary zone. Although their presence or absence in the centre of the oral part of the dorsum varies greatly, it is not a character of sufficient distinctness to be of value for purposes of classification.

The *Conical Papillae* vary in size and arrangement in the different families, and there are three types of the former:—

1. The papillae on the pharyngeal part of the tongue are small:—*Homo*, *Simia satyrus*.

2. The papillae on the oral part of the tongue are comparatively small, but those on the pharyngeal part are large and prominent:—*Gorilla gorilla*, *Anthropopithecus troglodytes*, all species of *Hylobates*, all species of *Lemur*, *Chiromys madagascariensis*, and *Tarsius spectrum*. This type also occurs in some lower Mammalia.

3. The papillae gradually increase in size from the apex of the tongue back to the epiglottis:—Cercopithecidae, Cebidae, Hapalidae, Lorisiidae, and Galagidae. This arrangement is also present in *Microcebus* in which the vallate papillae form a triangle, so the papillae are of value for distinguishing it from *Lemur*.

The arrangement of the papillae distinguishes most of the Cebidae from all other families. In the latter they form a cluster behind the apex and rows of varying degrees of obliquity behind

that, but in the Cebidæ they are dotted irregularly all over the dorsum.

The tongues with smooth non-papillary areas on the pharyngeal part of the dorsum have been enumerated above.

In most Primates the points on the oral part of the dorsum look backwards or backwards and inwards, but in some specimens of *Simia satyrus* and *Cercopithecus æthiops* those on the centre of the oral part run in all directions.

In the Cebidæ, Hapalidæ, Lemuroidea, and Tarsioidea the conical papillæ are mostly pointed, and cylindrical and globular forms are uncommon. In the other families there is a good admixture of all types.

The *Lateral Organs* present numerous forms and are of value for purposes of classification:—

1. Organs absent:—*Microcebus*, *Chironomys*, *Tarsius*, the Loriidæ and Galagidæ.

2. The laminae and sulci form ladder-like patterns on the dorsum of the tongue, and only their outer ends cut the lateral borders of the tongue:—*Gorilla gorilla* and *Simia satyrus*.

3. The organs are convex towards the lateral vallate papillæ:—*Anthropopithecus troglodytes*, *Hyllobates* (all species), *Lemur* (all species).

4. There are rows of short laminae and sulci on the lateral borders of the tongue:—Cercopithecidæ.

5. The inner borders of the organs are concave towards the lateral vallate papillæ:—Cebidæ.

6. A few faint irregular laminae and sulci are present on the lateral borders of the tongue:—Hapalidæ.

In very few specimens did I find an equal number of laminae and sulci in the two organs of the same tongue. But one must be careful not to mistake simple folds of the mucosa at either end of the organs for laminae. Histological examination is the only true test in doubtful cases, for it reveals the presence of taste-buds in the true laminae.

In a few species of *Cercopithecus* one may find fungiform papillæ situated on the laminae of the lateral organs.

The degree of protrusion of the laminae and depth of the sulci vary not only in different animals but in several examples of each.

The *Lingual Glands* are divided into apical and basal parts, but the former is most variable.

The *Apical Gland of Nuhn* is present only in *Homo* and *Simia satyrus*. Oppel believes that it is a piece which has become cut off from a forward prolongation of the basal glandular mass. The basal mass in the Marsupialia sends forwards two prolongations of variable stoutness, and it is possible that the Apical Gland of Nuhn has been cut off from one of these. If that were so it would support Gegenbaur's view that the tongues of the Primates have evolved from those of the Marsupialia.

The serous and mucous glands on the pharyngeal part of the

tongue are developed to an equal degree in the Primates, but the degree of development of the entire basal mass varies.

The pharyngeal part of the tongue possesses a variable degree of development of lymphoid nodules, and a variable number of orifices of pits and the ducts of glands; and the latter are of value for distinguishing the tongues of the various genera of the Cercopithecidæ from one another. Orifices are visible in all Cercopithecidæ, but are absent from most Cebidæ, so are of classificatory importance when taken in conjunction with the characters of the lateral organs and mode of arrangement of the conical papillæ. The following are the characters of the orifices in the Cercopithecidæ:—

Genus *Presbytes*:—Orifices larger and more patulous than in any other genus, and lie in the centres of large round glandular areas. The salivary glands are enormous.

Genus *Cercopithecus*:—Orifices well-marked, discrete and not patulous, and no white areas present around them.

Genus *Macacus*:—Orifices like pin points.

Genus *Cercocebus*:—Small duct orifices present at the sides of the base of the tongue.

Genus *Papio*:—Large duct orifices present at the sides of the base of the tongue.

In many of the Cebidæ the nodules on the base form zones, with concave anterior borders, in front of the epiglottis, but I did not observe a similar condition in any other family.

The *Frenal Lamella* varies greatly in the Primates, and appears to belong to the floor of the mouth rather than to the tongue. It varies even in several examples of the same species, so is of limited value for purposes of classification.

In *Homo*, *Simia satyrus*, and some specimens of *Symphatanus syndactylus* it appears as two simple folds over Wharton's Ducts; but Mr. Pocock informs me that he observed two well-marked processes in a young *Simia satyrus*. I cannot believe, however, in conformity with my observations on the tongues of other animals, that reduction in the lamella is a change due to advancing years. In other species the lamella appears as a triangular or tongue-shaped process with an entire or divided apex and with both edges entire, serrated, or bearing small sharp points. The sharpest and most prominent points on the edges occur in *Cercopithecus preussi* and some specimens of *Cebus fatuellus*.

The *Orifices of Wharton's Ducts* vary in their position on the lamella as follows:—

1. On the upper surface—*Gorilla gorilla*.
2. On the apex—*Anthropopithecus troglodytes*.
3. On the under surface—*Pithecia satanas*.

The apical position is the commonest form, however.

Tuckerman described a rich nerve plexus with peripheral nerve endings in the lamella of *Ateles ater*, and Gegenbaur considered that the endings were tactile in function. As this condition has

not been found in any other tongue there is insufficient material in which to work out its phylogenetic significance.

The *Sublingua*.—The various Lemuroidea are differentiated from one another by the shape, mobility, and characters of the crests and denticles as follows:—

1. *Sublingua* triangular or lyrate, has three ventral crests, and is very mobile. The apex is divided into a brushwork of denticles:—*Lemur*, *Hapalemur*, *Indrisidæ*.

2. *Sublingua* a large flat plate adherent to the under surface of the tongue by its central parts; no denticles present, but a strong keel-like ridge on its under surface projects forwards in the middle line:—*Chiromys*.

3. *Sublingua* large, tongue-shaped, but not quite so free as that of *Lemur*. There is only one median ventral crest, but the dorsal surface has a crest of variable prominence. This crest, the characters of the denticles, and the variations in the consistence of various parts of the *sublingua* are important:—

In *Microcebus* the *sublingua* is uniformly thick, the median dorsal crest is slight, and the denticles are moderately long.

In *Nycticebus* and *Loris* the central parts of the *sublingua* are thicker than the lateral parts, the median dorsal crest is small and the denticles are of moderate length; they are discrete in the former and close in the latter, but there is no essential difference between the *sublinguæ* of these genera.

In *Perodicticus* the median ventral crest is bifurcated posteriorly, the median dorsal crest is very prominent, and the denticles are long and slender.

In *Microcebus*, *Galago*, and *Hemigalago* the anterior border of the *sublingua* is broad, but in *Loris* and *Nycticebus* it is more or less pointed.

The *Plicæ Fimbriatæ* of the Simiidae are derived from the *sublingua* by a process of phylogenetic reduction, and I showed that the *plicæ* of *Anthropopithecus troglodytes* with the intervening piece of mucosa form a soft triangular field resembling a *sublingua*; this is even more marked in the tongue of the new-born child, as described and figured by Gegenbaur. The *plicæ* of *Phascolarctos cinereus*, however, do not bound such an area.

The tongues of the Gibbons, Cercopithecidae, Cebidae, and Hapalidae illustrate the ultimate stage of reduction, for no traces of the *sublingua* or *plicæ* are present as a rule in the extra-uterine stage. In the foetal Gibbon, as shown by Deniker, there is a well-marked *sublingua*; and I observed two minute *plicæ* in a young *Cercopithecus patas*, so it is probable that the foetuses of all Primates have *sublinguæ*.

If one examines a series of human tongues at different ages, one finds that the new-born child has well-developed *plicæ* or an actual *sublingua* provided with taste-buds. As age advances the buds disappear and the *plicæ* diminish in size. These taste-buds probably account for the more acute sense of taste in the child. Experimental methods also demonstrate that the sense of taste

elicited by applications of solutions to the centre of the oral part of the dorsum diminishes as age advances.

This atrophy of structure following loss of function may have played an important part in the reduction in and ultimate loss of the primitive Mammalian tongue.

The Lytta.—Two forms are to be recognised:—The lytta of the tongue and the lytta of the sublingua. And Gegenbaur showed that the latter, when present, appears in one of two forms. In *Stenops* it forms a strong central supporting rod, but in *Tarsius* it is double. In *Lemur* it is absent altogether. Owen described the keel on the ventral surface of the sublingua as the lytta, but sections through the tongue show a well-marked lytta inside; it is connected in the middle to the sublingua.

CLASSIFICATION.

The structures which are of value for purposes of classification are:—

1. The number and arrangement of the vallate papillæ.
2. The arrangement of the conical papillæ on the oral part of the dorsum.
3. The mode in which the conical papillæ increase in size from before backwards.
4. The size of the cluster of fungiform papillæ on the dorsum behind the apex of the tongue.
5. The characters of the lateral organs.
6. The width of the ventral papillary zone, with the number, characters, and arrangement of its papillæ.
7. The presence or absence and characters of the lyttæ of tongue and sublingua.
8. The presence or absence of the apical gland of Nuhn, and the characters of the orifices of ducts and pits on the pharyngeal part of the dorsum
9. The sublingua and plicæ fimbriatæ.

These features are of specific value in the case of all the Simiidae, except *Hylobates*, and many of the Lemuroidea, but they are of generic value only in all other Primates. They lend additional weight to some schemes of classification based on external and skeletal characters; in some cases they help us to settle points which are not supported by a large body of very conclusive evidence.

The tongue of *Simia satyrus* resembles that of *Homo* most closely. Both have rounded apices, and their form and general proportions are similar. They have no large conical papillæ on the base of the tongue, and their vallate papillæ form a V. The frenal lamellæ are two small folds over Wharton's Ducts, and their plicæ fimbriatæ are equally developed, but smaller than those of other Primates; and they are the only Primates possessing an Apical Gland of Nuhn. In *Simia satyrus* the lateral

organs are better developed, and the conical papillæ on the oral part of the dorsum include more pointed forms, but *Homo* alone of all the Primates possesses a foramen cæcum.

The ladder-like patterns formed by the lateral organs distinguish *Simia satyrus* and *Gorilla gorilla* from all other Simiidae which have organs convex towards the lateral vallate papillæ, but the tongue of *Gorilla gorilla* has enormous conical papillæ on the pharyngeal part of the tongue, large plicæ fimbriatæ, a median ventral crest, and a large triangular frenal lamella; it has no Apical Gland of Nuhn, and its vallate papillæ form a V or Y.

The only character which really differentiates *Anthropopithecus troglodytes* on the one hand from *Hylobates* and *Symphatanus* on the other is the possession of plicæ fimbriatæ, for there is a similarity between them in all other features; and *Hylobates* has a well-marked, triangular, bifid lamella, whereas *Symphatanus syndactylus* has two small folds over Wharton's Ducts similar to those of *Homo* and *Simia satyrus*. Their vallate papillæ form a Y.

In the Cercopithecidae, Cebidae, and Hapalidae the vallate papillæ never form a Y, the conical papillæ on the base of the tongue are never disproportionately large, and the lateral organs are neither ladder-like nor convex towards the lateral vallate papillæ. The chief differences between them lie in the characters of the lateral organs, the size of the apical cluster of fungiform papillæ, and the mode of arrangement of the conical papillæ on the oral part of the dorsum.

In the Cercopithecidae the lateral organs form rows of laminae and sulci on the lateral borders, the apical cluster of fungiform papillæ is large, and the conical papillæ on the oral part of the dorsum are regularly arranged. The genera are distinguished by the characters of the orifices of ducts and pits on the pharyngeal part of the dorsum (page 762).

In the Cebidae the inner borders of the lateral organs are concave towards the lateral vallate papillæ, the conical papillæ on the oral part of the dorsum are crowded together without any definite arrangement, and the apical cluster of fungiform papillæ is small.

The vallate papillæ are two in number, and there is a well-marked median sulcus on the pharyngeal part of the dorsum in *Aotus*, but in all other genera there are more than two vallate papillæ, but no basal dorsal sulcus.

The ventral papillary zone is wide, and has few fungiform papillæ in *Lagothrix*, but it has many papillæ in *Ateles* and *Cebus*. In *Ateles* the ventral fungiform papillæ are most numerous round the apex, but in *Cebus* they are most numerous farther back.

The ventral papillary zone is narrow in *Pithecia*, *Alouatta*, *Callicebus*, and *Cacajao*. It has many fungiform papillæ in *Pithecia* but few or none in the others; and *Alouatta* is the only

genus possessing large glandular orifices on the base of the tongue. *Callicebus* has many nodules and few orifices on the base, but *Cacajao* has neither.

The Hapalidæ always have a vallate triangle and a few irregular laminae and sulci in their lateral organs. The pharyngeal part of the tongue occupies a relatively small part of the whole, and the ventral papillary zone is small or absent. The conical papillæ are regularly arranged and the apical cluster of fungiform papillæ is small. The lingual characters are not sufficiently distinctive to classify the genera.

The Lemuroidea and Tarsioidea differ from the Simiæ in the possession of a sublingua whose size, consistence, mobility, denticles, and minute structure vary in different families.

In the Tarsioidea the sublingua is soft, small, devoid of denticles, and only delimited at the sides from the under surface of the tongue by a narrow groove. There are no lateral organs, no large conical papillæ, and few apical fungiform papillæ.

In the Lemuroidea the sublingua is large, horny, denticulated, and is more or less movable.

In *Lemur* and *Hapalemur* the sublingua is triangular or lyrate, very free, and has three ventral crests. No lytta is present. The vallate papillæ form a Y, and the conical papillæ on the base are disproportionately large. The lateral organs are convex towards the lateral vallate papillæ.

In *Chiromys* the sublingua is tongue-shaped, adherent by its central parts, has one ventral crest which is keel-like and nodulated. It has a lytta inside the tongue. Vallate papillæ form a pair or triangle, but never a Y. Conical papillæ on base of tongue large. No lateral organs.

In *Microcebus*, the Lorisidæ and Galagidæ the sublingua is a flat plate with one median ventral crest and a variable dorsal crest. It varies in mobility, consistence, and denticles, and the value of these characters has already been described (page 763). The vallate papillæ form a triangle, but never a Y, the conical papillæ on the base of the tongue are not disproportionately large, and lateral organs are absent.

The special points arising from these notes on classification are:—

1. The tongue of *Simia satyrus* resembles that of *Homo*.
2. *Simia satyrus* and *Gorilla gorilla* differ from all other Simiidæ in the characters of the lateral organs, but there the resemblance between these two species stops.
3. The tongue of *Hylobates* differs from that of *Anthropopithecus troglodytes* in having no plicæ.
4. The separation of *Symphalangus* from *Hylobates*.
5. The great value of the lateral organs for purposes of classification.
6. The value of the lingual glands for distinguishing between the genera of the Cercopithecidæ.

7. The genera of the Hapalidæ cannot be distinguished from one another by the characters of the tongue.

8. The tongues of *Lemur* and *Hapalemur* resemble those of the Simiidæ most closely.

9. It is impossible to ally the tongue of *Microcebus* with those of *Lemur* and *Hapalemur*, but it resembles those of the Lorisidæ and Galagidæ.

10. The characters of the tongue at once distinguish the Lorises, Galagos, and Pottos from *Lemur*.

11. The tongue of *Tarsius* resembles neither those of the Simiidæ nor of *Lemur*, and is hard to distinguish from those of the Lorisidæ and Galagidæ. It has three vallate papillæ in a line, but these may be elements of a triangle which has been flattened out.

12. The keel on the under surface of the sublingua is not the true lytta as described by Owen.